THE SYSTEMATICS AND DISTRIBUTION OF THE HOGNOSE VIPER *BOTHROPS NASUTA*[1] BOCOURT (SERPENTES: VIPERIDAE)

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ABSTRACT

Variation in selected characters of scutellation, coloration, and body proportions in the Neotropical hognose viper, *Bothrops nasuta* Bocourt, is discussed and the speciied is redescribed. Analysis of this variation allows for the definition of three distinctive populations. No infraspecific taxa are recognized. The biogeographic history of the species is also discussed.

INTRODUCTION

Bothrops nasuta Bocourt, 1868, is a small, terrestrial pit viper occurring in humid lowland forests from Chiapas, México southward to Ecuador. It is a member of the *Bothrops lansbergi* group, a group of hognose vipers (*sensu* Burger, 1971), which was last revised by Amaral (1929a). The hognose viper group is in need of systematic study and the acquisition of an unusual specimen of *B. nasuta* from Ecuador by one of us (LP) prompted a review of the systematics of this species, the most widespread member of the group.

Amaral (1929a) had 32 specimens available to him. Since his revision more material has become available allowing for a more complete understanding of the systematics of this species.

MATERIAL AND METHODS

We examined 241 specimens of *Bothrops nasuta*. The single specimen of this species from Belize (Neill, 1965) was not available to us. The following scales were counted using the definition of Klauber (1972): intercanthals, prefoveals, preoculars, suboculars, and postoculars. We follow Burger (1971), with some modification, in defining and recording the following scales: postcanthals, interictals, interoculars, oculabials, and nasorostrals. The definitions of these latter scales are as follows:

Postcanthals. The undifferentiated marginal head scale(s) contacting the upper preocular between the canthal and supraocular.

Interictals. The supracephalic scales occupying the posterior portion of the head from oral rictus to oral rictus. For consistency, the interictals were counted between the last supralabials.

Interoculars. The irregularly disposed scales in the frontal region that were counted along the path between the supraoculars that traverses the fewest scales.

Oculabials. The rows of scales between

[1]According to Shreve (1957), Amaral (1964a, 1964b, 1976) and Schwartz and Thomas (1975), generic names ending in *-ops* are feminine in classical Greek usage. Thus, the specific name for this hognose viper is *nasuta*, not *nasutus*. For opinions to the contrary, see the 1964 edition of the International Code of Zoological Nomenclature and Smith and Larsen (1974).

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suboculars and supralabials but including neither.

Nasorostrals. The scales between the nasal and rostral.

The number of ventral scales was counted using the method of Dowling (1951). Due to the irregularity of scutellation in the nasofrontal area, the scales anterior to and including the interoculars, except for those bordering the edge of the head (rostral, internasals, canthals, postcanthals, and supraoculars), were counted and given the name nasofrontals. Postfoveals and median gulars were not counted due to their high degree of variability and consequent difficulty of accurate tabulation. The dorsal scale rows were counted one head length posterior to the interictals, at midbody, and at the vent. All measurements were made on preserved specimens, with the exception of those made on a record-length specimen from Ecuador in the senior author's live collection.

Statistical analyses were accomplished using the Student's *t* test, as described by Simpson, et al. (1960), using a probability value of .95.

Inasmuch as *Bothrops nasuta* has a basically linear distribution, we used, for the sake of convenience, the political boundaries within the animal's range as the basis for subdividing for analysis our data on variation. The populational groupings in the tables are defined in the discussion.

HISTORICAL SUMMARY

A considerable amount of confusion has existed in the literature concerning the hognose vipers. Much of the confusion was largely eliminated by Amaral's paper (1929a) on the *Bothrops lansbergi* group. In that paper Amaral redescribed *Bothrops nasuta* Bocourt and demonstrated its distinctness from *B. lansbergi* (Schlegel). He also snyonymized *B. brachystoma* (Cope) with *B. lansbergi*, thus terminating the application of the name *brachystoma* to specimens of *B. nasuta*. Moore (1962), however, incorrectly placed *brachystoma* as a synonym of *B. nasuta*.

Cope (1876) described *Bothriopsis proboscideus*. Later, he (1879) questioned the validity of *B. proboscideus* but continued to recognize it in a later paper (Cope, 1887). Amaral (1929a) placed *B. proboscideus* in the synonymy of *Bothrops nasuta*.

Posada-Arango (1889a) proposed a new genus of solenoglyph snakes, *Thanatos*, and described several new species, including *T. sutus*. Later in the same year (1889b) he introduced the generic name *Thanatophis*, without explanation (*fide* Vanzolini, 1977). Nicéforo María (1938) concluded that *Thanatophis sutus* is probably a synonym of *Bothrops nasuta*. His decision was tentative due to Posada-Arango's generalized description. García (1896), using the nomenclature of Posada-Arango, figured a specimen identified as *Thanatophis sutus*, which is actually a juvenile *B. nasuta*, supporting the contention that the two names are synonymous, a supposition supported by Daniel (1949, 1955), Burger (1971), and us. Peters and Orejas-Miranda (1970) and Vanzolini (1977) incorrectly place *Thanatophis* (or *Thanatos*) *sutus* as a synonym of *Bothrops lansbergi*.

Burger (1971) subdivided the various members of the genus *Bothrops* (*sensu lato*) into five genera. *Bothrops nasuta* was placed in the genus *Porthidium* as *P. nasutum*. This disposition was accepted by Smith and Smith (1976). Whereas we are in fundamental agreement with the generic limits proposed by Burger (1971), we prefer not to use them inasmuch as an adequate analysis of the basis for such a classification was not presented by him. In addition, Burger (1971) recognized two subspecies, *nasutum* and *sutum* (=*nasuta* and *suta*). This disposition was unsupported with any data and is not followed by us (see analysis of variation).

SPECIES ACCOUNT

Bothrops nasuta Bocourt

Bothrops lansbergii: Günther, 1863: 350; Dunn, 1928: 30 (part); Picado.1936: 392; E. H. Taylor, 1951: 178, 1954: 681.

Bothrops nasutus Bocourt, 1868: 202 (type locality: Panzós, on the banks of the Río Polochic, Guatemala; holotype: MNHN 1592 - *fide* Stuart, 1963), 1876: 410; Barbour and Loveridge, 1929: 3; Smith, 1943: 400, 1958: 224; Smith and Taylor, 1945: 182; Stuart, 1948: 87, 1950: 24, 1958: 29, 1963: 130; E. H. Taylor, 1954: 783; Moore, 1962: 62; Duellman, 1963: 245, 1966: 705; Klemmer, 1963: 408; Neill, 1965: 113; Hoge, 1965: 127; Savage, 1966: 751, 1973: 17; Heyer, 1967: 267; Moore, et al., 1968: 48, 61; Meyer, 1969: 415; Minton and Minton, 1969: 207; Scott, 1969: 232; Peters and Orejas-Miranda, 1970: 49; Hoge and Romano, 1971: 252; Alvarez del Toro, 1973: 158; R. T. Taylor et al., 1974: 384, 388; Henderson and Hoevers, 1975: 51; Campbell, 1976: 153.

Porthidium nasutus: Cope, 1871: 207.

Porthidium nasutum: Cope, 1871: 207, 1876: 151, 1879: 271, 1887: 89; Smith and Smith, 1976: S-B-16.

Bothriopsis proboscideus Cope, 1876: 150 (type locality: Sipurio, at base of mountains, Costa Rica; no holotype designated); Cope, 1879: 271.

Bothrops lansbergi: Müller, 1878: 703 (in error).

Bothrops brachystoma: Müller, 1882: 154; Amaral, 1925: 29, 1927a: 22, 1927b: 47; Loveridge, 1928: 63.

Bothriopsis (sic) *proboscideus*: Cope, 1887: 89.

Brothriopsis brachystoma: Cope, 1887: 89 (part).

Thanatos sutus Posada-Arango, 1889a: 45-49 (paper not seen).

Thanatophis sutus Posada-Arango, 1889b: 344 (type locality: "le district de Zea," Colombia; no holotype designated); García, 1896: 26.

Bothriechis lansbergii: Gunther, 1895: 190 (part).

Lachesis brachystoma: Boulenger, 1896: 547 (part); Boettger, 1898: 139.

Trimeresurus brachystoma: Mocquard, 1909, 945 (part).

Bothrops nasuta: Amaral, 1929a: 25. 26, 1929b: 237, 1931a: 89, 1931b: 94, 1935: 22, 1944a: 7, 10, 1944b: 18; Picado, 1931a: 69, 1931b: 104, 1936: 391; Dunn and Emlen, 1932: 32; Dunn, 1933: 79, 1944: 215; Schmidt, 1933: 19; Wettstein, 1934: 38; Nicéforo Maria, 1938: 419, 1942: 101; Prado, 1939: 1; Rendahl and Vestergren, 1941: 16, Daniel, 1949: 329, 1955: 80; Pifano and Römer, 1949: 302; E. H. Taylor, 1951: 177; Peters, 1960: 510; Villa, 1962: 50; Brattstrom 1964: 189; Medem, 1968: 194; Minton and Minton, 1969: 216; Wilson and Meyer, in press.

Trimeresurus nasutus: Dunn and Bailey, 1939: 20; Smith, 1941: 62.

Porthidium nasutum nasutum: Burger, 1971: 35, 132.

Porthidium nasutum sutum: Burger, 1971: 35, 132.

Description - The scutellation of this species is as follows: rostral higher than wide, the ventrolateral portion infrequently separated off as a nasorostral (5.0% of specimens examined); internasals paired, elongate, elevated anteriorly, usually in contact (81.4%); canthals usually single (96.6%); postcanthals often one (67.7%), sometimes two; intercanthals 3-7 (x=4.95); nasofrontals 20-59 ($\bar{x}$=37.23); interoculars 3-7 ($\bar{x}$=5.19); lateral edge of supraoculars flattened; interictals 19-28 ($\bar{x}$=24.58); nasal scale partially divided; prefoveals 2-12 ($\bar{x}$=5.60); subfoveals 1-7 ($\bar{x}$=2.26); loreal wider than high, upper preocular large, extending dorsally over the canthal ridge; middle preocular divided or not, infrequently absent, in contact with orbit or not; lower preocular single, in-

frequently absent, in contact with orbit or not; suboculars 1-4 ($\bar{x}$=1.66); postoculars 1-4 ($\bar{x}$=2.30); oculabials 1-4, usually 2 (88.8%); supralabials 8-11 ($\bar{x}$=9.34); infralabials 9-13 ($\bar{x}$=11.41), the first pair usually in contact; a single pair of chinshields; ventrals 123-145 ($\bar{x}$=135.80); anal plate single; subcaudals entire, 24-41 ($\bar{x}$=30.02); tail not prehensile; dorsal scale rows at neck 23-29, usually 25 (87.8%), at midbody 21-27, usually 23 (92.8%), at vent 17-21, usually 19 (96.6%); apical pits absent.

The hemipenis is divided with a bifurcate sulcus spermaticus, the sulcus dividing close to the base of the organ and each branch extending to the distal end of the apical lobe. The basal portion of the organ and the areas lateral to and between the branches of the sulcus are spinulate. The shoulders and the absulcate side of the organ are covered with spines which increase gradually in size proximally, terminating with a pair of enlarged basal spines situated on either side of the sulcus. Distal areas of the apical lobes are calyculate with papillate micro-ornamentation.

Distribution and Ecology - *Bothrops nasuta* is an inhabitant of the humid lowlands of Middle America and adjacent northwestern South America (Figs. 1 and 2). *Bothrops nasuta* belongs to the Eatern Mesoamerican Complex of Savage (1966) and the Humid Tropical Assemblage of Duellman (1966). It is distributed along the Caribbean lowlands from northern Chiapas, México, eastward through northern Guatemala, possibly to Belize (see discussion below), thence southward through Central America (Fig. 1) and onto the Pacific coastal plain of western Columbia to midwestern Ecuador (Fig. 2). The species probably also occurs in the mesic lowlands of eastern Veracruz, México, inasmuch as it has been recorded near the border in Chiapas in the same type of forest (Alvarez del Toro, 1973). A specimen (ANSP 4873) recorded from "Veracruz, Mexico" shows characters of specimens from much farther south in the range and we regard the data as questionable. The species probably also occurs in the southern portions of Tabasco.

The occurrence of *Bothrops nasuta* in Belize is questionable. Schmidt (1941) recorded a specimen of a hognose viper from Benque Viejo, Cayo District, Belize, which he identified as *Trimeresurus yucatanicus*. Neill (1965) recorded a specimen of *B. nasuta* from Xuantunich (=Benque Viejo), Cayo District, and speculated that Schmidt's specimen was probably of the latter species. This disposition was followed by Henderson and Hoevers (1975). McCranie and Porras (1978) examined the Schmidt specimen (USNM 61781), however, and determined it to be *Bothrops yucatanica*, thus reestablishing the occurrence of this species in Belize. The description of the specimen reported by Neill (1965) is ambiguous and will not distinguish *B. nasuta* from *B. yucatanica*.

In the northern part of its range (the Mexican and most of the Guatemalan portion), *B. nasuta* lives in the broadleafed forest or quasi-rainforest division of the evergreen forest (c.f. Duellman, 1966; also see Stuart, 1966). Duellman (1966) characterized these forests as having a marked dry season at which time some of the trees become leafless. However, some rain apparently falls throughout the year (Duellman, 1963). Stuart (1958) considered the forests of El Petén, Guatemala, as representing a transition from the wet forests of the south and the dry forests of the outer Yucatán Peninsula to the north. *Bothrops nasuta* apparently adapts to the drier conditions of the quasi-rainforest by living in thick woods around marshy areas (Alvarez del Toro, 1973), in the vicinity of rivers where the forests are more mesic (Chamá, 12 km NW Chinajá, Panzós, Piedras Negras, and Sayaxché, Guatemala), under similar conditions around Lago Miramar, Chiapas, México, and in the high forests surrounding the *aguadas*

of the Petén region of Guatemala. From extreme eastern Guatemala southward throughout Central America, the range of *B. nasuta* is within the more humid tropical rainforest division of the evergreen forest (c.f. Duellman, 1966). This forest differs from the quasi-rainforest in that the habitat is at least moderately moist throughout the year even though rainy and dry seasons are evident. These moist conditions are enhanced by the tendency of the forest to develop a continuous treetop canopy which provides abundant shade creating the "greenhouse effect" discussed by Duellman (1966). The only known occurrence of *B. nasuta* outside the evergreen forest is in the scrub forest (c.f. Duellman, 1966) of the Sula Plain near San Pedro Sula, Honduras. However, we believe these specimens came from gallery forest associated with the rivers of the region.

In several places in Costa Rica and Panamá, *Bothrops nasuta* crosses the Continental Divide onto the Pacific versant. The species has been collected on both sides of the divide in the Tilarán area of Guanacaste Province, Costa Rica. Along the Tilarán transect studied by heyer (1967), the range of *B. nasuta* is apparently continuous across the low divide (850 m) onto the Pacific versant, where the species has been collected approximately 4 km west of the divide. One

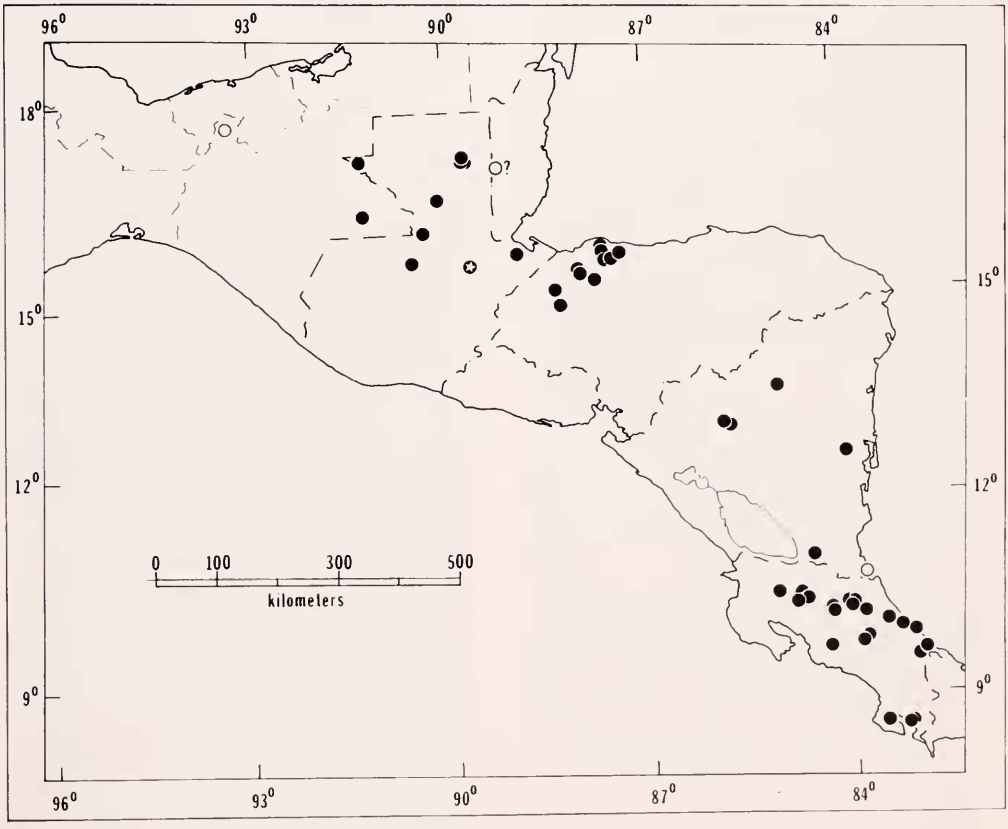

Figure 1. Distribution of *Bothrops nasuta* in Central America. Solid symbols represent localities of specimens examined. Hollow circles represent literature records (see section on distribution and ecology for discussion of questioned locality in Belize). The type locality is indicated by a star within a circle.

specimen (UCR 110) was collected on the Pacific versant at Puriscal (=Santiago), San José Province, Costa Rica. This specimen represents a relict population. An isolated population also occurs on the Pacific lowlands of the Golfo Dulce area of Costa Rica and probably adjacent Panamá. Savage (1966) and Savage and Vial (1974) discussed the factors creating the isolation of the vegetation of this region. However, the herpetofauna of the Golfo Dulce area resembles that of the Caribbean lowlands of Costa Rica and Panamá (Duellman, 1966; Savage, 1966; Savage and Vial, 1974). In Panamá, *B. nasuta* has been collected on the Pacific versant close to the Continental Divide in El Valle de Antón, Coclé Province. Dunn (1933), in a discussion of the El Valle area, stated that "Atlantic side conditions and fauna come a little way over the divide onto the Pacific versant." Two specimens collected by Herbert Clark (MCZ 37115-16) are recorded from Panama City, Panamá. Panama City is located in a savanna habitat (c.f. Duellman, 1966). These two specimens probably came from farther north in the mesic forests of the Canal Zone area where Clark obtained 13 other specimens. No specimens are available from Panamá east of the Canal Zone area, but it undoubtedly occurs in the Caribbean mesic forests of eastern Panamá.

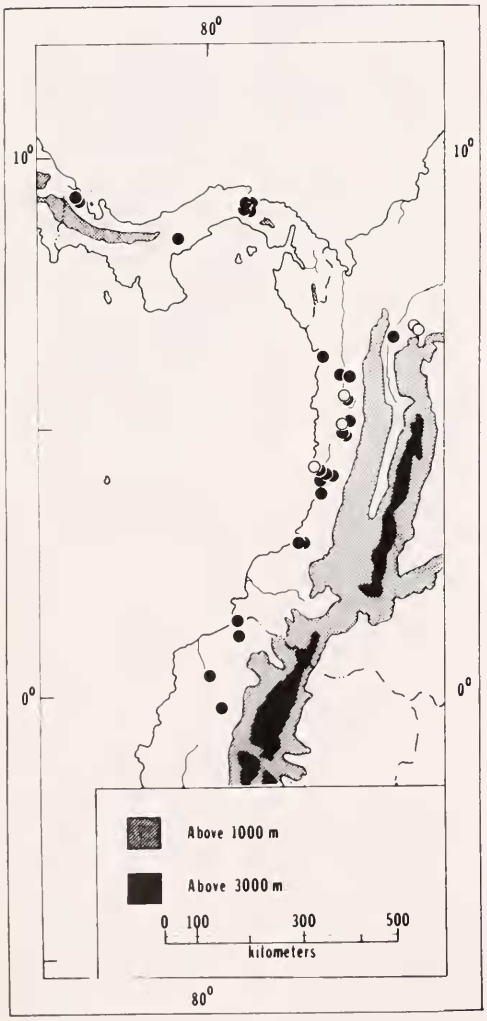

Figure 2. Distribution of *Bothrops nasuta* in Pananá, Colombia, and Ecuador. For explanation of symbols see Figure 1.

In South America *Bothrops nasuta* inhabits the lowland rainforests of Colombia west of the Andes southward to midwestern Ecuador. Dunn (1940), Duellman (1966), and Savage (1966) discussed the "crossover effect" occurring in the eastern Panamá-northwestern Colombia region, where the Caribbean mesic forms of lower Central America cross onto the wet Pacific lowlands of Colombia. However, the Pacific lowlands consist of a very narrow strip in northwestern Colombia. The lowland rainforests east of the Andes in the central portion of the department of Chocó and the adjacent western part of the department of Antioquia, Colombia, which are also inhabited by *B. nasuta*, are drained by the Río Atrato and its tributaries, which then flow northward into the Caribbean Sea. It is not until the Río San Juan drainage of southern Chocó is reached that *B. nasuta* becomes essentially a Pacific coastal plain animal, which it then remains to the terminus of its range in midwestern Ecuador. *Bothrops nasuta* also inhabits the low-

land rainforests of the rios Cauca and Porce in the department of Antioquia, Colombia. As with the Río Atrato, these latter two rivers flow northward into the Caribbean. The forests along the eastern edge of the Andes and on the Pacific coastal plain of Colombia are one of the most humid areas of the world and certainly the most humid of all of South America (Eidt, 1968; Haffer, 1970). The rains in the Quibdó area, Chocó, Colombia, fall year around (Haffer, 1970). Eidt (1968), in describing central Chocó, Colombia, stated that "only for a few days each year, usually when winds from the north disturb the general calm of the region, are there brief respites from the near constant rains." Myers et al. (1978) discussed the habitat at Quebrada Guanguí, Depto. Cauca, Colombia, where they collected a series of *B. nasuta* (AMNH 109794-811).

Bothrops nasuta occurs from near sea level to about 900 m in elevation, but is generally found below the 600 m contour. Of 112 specimens with elevational data, 49 (43.8%) were from below 200 n and 107 (95.5%) were from below 625 m The highest elevation datum available i 900 m for two specimens (UMMZ 116523, 117735) from near Matagalpa Nicaragua. Dunn (1944) gave an eleva tion of 1885 m for *B. nasuta* based on a record for Urrao, Antioquia, Colombia (Nicéforo María, 1938, 1942). We doubt that the specimen actually came from this elevation. Nicéforo Maria (1938) stated "que le fueron remitidos de. . .." This literally means "received from," which we interpret to mean "shipped from." We also question two other Nicéforo María (1938, 1942) records; Pueblo Rico, Depto. Caldas and Medellín, Depto. Antioquia. The elevations of these last two places are 1500 and 1538 m, respectively (Medem, 1965). Of 24 Colombian specimens with elevational data, all were from 200 m or below.

Bothrops nasuta is both terrestrial and nocturnal, although specimens can be found sunning themselves by day (Smith, 1943; pers. observ.). The species can also be found on low bushes or shrubs (E. H. Taylor, 1954; Medem, 1968). Posada-Arango (1889b) mistakenly believed that *B. nasuta* is arboreal, as did Amaral (1927b), when he said that *B. brachystoma* (=*B. nasuta*) "is a tree viper." Specimens have been found inside cavities in the trunks of trees, underneath roots of trees or rocks, on top of piles of rubbish (Alvarez del Toro, 1973), under rotting logs (Stuart, 1958), inside huts (Stuart, 1948), among loose rocks of ruins, (Smith, 1943), or simply on the forest floor (Duellman, 1963). We have collected *B. nasuta* under and lying near logs in the Turrialba area of Costa Rica.

Picado (1931a) reported that newborn *Bothrops nasuta* will eat earthworms and later will consume small lizards of the genus *Anolis*. Amaral (1927b) stated that the species feeds on lizards and Alvarez del Toro (1973) indicated that it feeds on anoles and mice. Picado (1931a) reported an instance of cannibalism involving juveniles. We have observed cannibalism among adults and juveniles in captivity. We have also observed them to eat leopard frogs (*Rana* sp.), anoles (*Anolis* sp.), and mice in captivity.

Bothrops nasuta has been reported to have 8 to 18 young (Picado, 1931a). A specimen in our collection (now LSUMZ 36898) from near Turrialba, Costa Rica, gave birth to 14 young in September, 1967.

Bites from *B. nasuta* are known to cause fatalities in human beings (Daniel, 1949), although Minton and Minton (1969) did not believe they are capable of doing so.

ANALYSIS OF VARIATION

Twenty-six characters were analyzed for geographic, sexual, ontogenetic, and individual variation. These characters are discussed below.

Internasals. - Typically, *Bothrops*

nasuta has the internasal scales in medial contact or separated by only one scale. One specimen (FMNH 68056), however, has the internasals separated by two scales. This specimen also has one shortened and one elongate internasal scale. Two specimens (LACM 45413, 45416) from Colombia do not have the internasal scales as elevated as do other *B. nasuta*, but are typical in all other respects.

The frequency of medial contact of the internasals varies geographically. All of the specimens of *B. nasuta* from México southward to Nicaragua have their internasals in mutual contact. Three specimens from Costa Rica and one from adjacent northwestern Panamá have their internasal scales separated by one scale, but two of these specimens are from the Península de Osa. The frequency of the mutual internasal contact is reduced in specimens from central Panamá southward to Ecuador (Table 1). In addition, specimens from central Panamá and Ecuador have the internasals in contact less frequently than do specimens from Colombia. In all of the specimens but one, which is a juvenile, from the Península de Osa, the internasals are less elevated and the snout is more attenuate.

Nasofrontals. - The numbers of nasofrontal scales in male *B. nasuta* average slightly lower than in females (Table 2) but the differences are not statistically significant.

Specimens from central Panamá exhibit a high average number of nasofrontal scales relative to other areas of the range (47.21 ± 2.63 as opposed to 37.79 ± 0.89).

Intercanthals. - Males average fewer intercanthals than do females (Table 3), except in central Panamá, but the latter differences will probably be reversed with study of additional material.

Central and western Panamanian specimens have a higher average number of intercanthals than do specimens from the remainder of the range (5.48 ± 0.36 vs. 4.92 ± 0.10).

Interoculars. - The average number of interoculars is higher in females than in males in the entire sample but the differences are not statistically significant (Table 3). However, specimens from the northern portion of the range (western Panamá northward), excepting the Península de Osa, show no statistically significant average difference between the sexes, whereas those from that point southward do (Table 3).

Interictals. - Generally, males have fewer interictals than do females but the differences are not statistically significant (Table 3).

Rostral. - Two specimens (AMNH 10981, UMMZ 91078) have the rostral scale horizontally divided. All other specimens have a single rostral scale.

Nasorostral. - A nasorostral scale is occasionally present in specimens from disparate parts of the range. The incidence of females possessing this scale appears to be greater than that of the males, inasmuch as ten of the twelve specimens having 1 or 2 nasorostrals are females.

Nasal. - All specimens of *B. nasuta* examined have a partially divided nasal scale, except for two, which have the scale completely divided. The usual condition is that of a partial crease at the upper and lower sections of the scale but a few specimens exhibit a complete division of this scale above or below the naris.

Prefoveals. - One specimen (UMMZ 117735) has the prefoveal scales extending to the rostral scale thus excluding the nasal scale from contact with the first supralabial.

Females have more prefoveals on the average than do males throughout the range (Table 4).

Subfoveals. - With respect to the sample as a whole, males have significantly fewer subfoveals than do females (Table 4).

Preoculars. - There are generally an upper, middle, and a lower preocular

Table 1. Variation in internasals, body blotches, and sex ratios in Bothrops nasuta (parenthetical numbers in first and last columns indicate sample size; middle columns indicate range, mean, confidence limits, and sample size, where applicable)

	Internasals	Body blotches		Sex ratios
	% in contact	Males	Females	% of females
México	100(2)	-	17	100(2)
Guatemala	100(13)	18-22(19.29±1.16)7	15-17(15.75±0.74)8	61.1(18)
Honduras	100(16)	17-20(18.50±19.06)2	15-18(15.88±0.94)8	81.3(16)
Nicaragua	100(7)	17-19(17.67±2.88)3	16	57.1(7)
Costa Rica	98.9(95)	16-22(18.36±0.63)25	15-20(17.22±0.48)36	60.0(95)
Western Panamá	90.0(10)	19-22(20.00±4.30)3	16-19(18.20±1.04)5	70.0(10)
(Northern Population)	98.6(148)	16-22(18.60±0.49)40	15-20(16.90±0.33)60	63.5(148)
(Osa Population)	71.4(7)	18-20(19.0±12.71)2	15-19(16.67±5.18)3	57.1(7)
Central Panamá	22.2(18)	19-23(19.00±4.68)4	16-19(17.77±0.70)13	78.9(19)
Colombia	66.7(57)	15-23(19.31±0.77)26	15-22(18.61±0.66)25	52.6(57)
Ecuador	22.2(9)	17-20(19.00±1.52)5	17-18(17.75±0.80)4	44.4(9)
(Southern Population)	52.4(84)	15-23(19.23±0.66)35	15-22(18.26±0.45)42	57.6(85)
Totals	81.6(239)	15-23(18.90±0.39)77	15-22(17.44±0.29)105	61.3(240)

(95.0% of the specimens examined). The contact of the preoculars with the orbit is inconsistent, expecially since there is often a fleshy rim of tissue interposed between the preoculars and the orbit. Individual specimens exhibit different preocular arrangements on either side of the head. There are occasional specimens that do not have a middle preocular. This condition usually occurs when the upper and lower preoculars are enlarged and in contact with each other, thus excluding the middle one from orbital contact. In one specimen (MCZ 55069) an enlarged supralacunal takes the place of the middle preocular.

Suboculars and Postoculars. - The subocular and postocular scales vary in number (see description). In many specimens counts varied widely from one side of the head to the other. Specimens had as few suboculars as one or as many as four and postoculars range from two to four on either side of the head of the same animal.

Oculabials. - The usual number of oculabials present in *B. nasuta* is two (88.8% of specimens examined).

Male *B. nasuta* from the entire range have significantly fewer oculabial scales than do females (Table 5).

The number of specimens in which the

Table 2. Variation in ventrals, subcaudals, and nasofrontals in Bothrops nasuta (parenthetical numbers indicate range, mean, confidence limits, and sample size, where applicable)

	Ventrals		Subcaudals		Nasofrontals	
	Males	Females	Males	Females	Males	Females
México	-	138	-	29-30(29.50±6.35)2	-	28-32(30.00±25.41)2
Guatemala	138-141(139.14±0.99)7	140-145(142.27±1.09)11	34-38(35.57±1.17)7	28-32(29.64±0.16)11	26-39(31.14±3.80)7	29-43(37.18±3.59)11
Honduras	135-139(137.33±5.17)3	135-142(139.67±1.47)12	33-35(34.33±2.88)3	26-30(27.91±0.70)11	26-46(36.00±127.06)2	29-48(34.92±3.52)12
Nicaragua	139-142(140.33±3.80)3	136-140(138.50±2.76)4	28-33(30.50±31.77)2	27-29(28.00±1.84)4	33-35(33.67±2.87)3	32-46(38.50±9.23)4
Costa Rica	129-143(136.37±0.84)38	128-144(137.35±0.42)57	27-41(32.67±0.72)36	24-35(28.46±0.18)54	22-43(33.53±1.69)38	25-54(35.05±1.54)56
Western Panama	133-138(136.00±6.60)3	129-139(135.29±3.65)7	34-36(35.00±2.48)3	25-31(27.86±1.63)7	39-42(41.00±4.30)3	33-46(40.86±4.61)7
(Northern Population)	129-143(136.98±0.71)54	128-145(138.14±0.55)92	27-41(33.22±0.65)51	24-35(28.49±0.46)89	22-46(33.77±1.48)53	25-54(35.78±1.20)92
(Osa Population)	136-137(136.67±1.43)3	136-139(137.25±2.39)4	33(33.00±0)2	25-27(26.25±1.52)4	20-34(28.33±12.95)3	33-40(36.25±4.75)4
Central Panamá	129-131(130.25±1.52)4	130-139(134.47±1.34)13	30-34(31.00±3.18)4	26-32(28.86±0.96)14	38-53(48.18±10.43)4	39-59(46.90±2.93)15
Colombia	123-141(130.54±1.37)26	127-143(132.83±1.31)29	28-35(32.00±0.60)27	24-31(28.07±0.59)30	25-56(39.22±3.37)27	29-58(41.43±2.56)30
Ecuador	127-137(131.00±4.65)5	132-136(133.50±3.05)4	31-35(33.00±1.96)5	28-29(28.50±0.92)4	32-44(39.20±5.72)5	31-45(40.25±10.18)4
(Southern Population)	123-141(130.57±1.10)35	127-143(133.35±0.92)46	28-35(32.03±0.55)36	24-32(28.33±0.45)48	25-56(40.14±2.77)36	29-59(42.84±1.92)49
Totals	123-143(134.53±0.28)92	127-145(136.56±0.58)142	27-41(32.73±0.44)89	24-35(28.38±0.33)141	20-56(36.09±1.54)92	25-59(38.17±1.12)145

Table 3. Variation in intercanthals, interoculars, and interictals in Bothrops nasuta (explanations as for Table 2)

	Intercanthals		Interoculars		Interictals	
	Males	Females	Males	Females	Males	Females
México	-	5(5.00±0)2	-	4-6(5.00±12.71)2	-	25-27(26.00±12.71)2
Guatemala	4-5(4.43±0.47)7	5-6(5.09±0.20)11	5-6(5.29±0.45)7	3-6(4.55±0.63)11	23-26(24.86±0.83)7	23-26(25.09±0.70)11
Honduras	4-5(4.33±1.40)3	4-6(4.92±0.46)13	3-5(4.33±2.87)3	3-7(4.31±0.71)13	25-27(25.67±2.87)3	23-27(24.85±0.73)13
Nicaragua	5(5.00±0)3	5-6(5.50±0.92)4	5(5.00±0)3	5-7(6.00±1.30)4	23-25(24.00±2.48)3	24-27(25.50±2.05)4
Costa Rica	3-6(4.53±0.23)38	4-7(4.89±0.15)57	4-7(5.21±0.26)38	3-7(5.35±0.20)57	19-27(24.00±0.53)38	19-28(24.51±0.41)57
Western Panamá	4-6(5.00±2.48)3	5-7(5.71±0.88)7	5-7(6.33±2.87)3	5-7(5.86±0.34)7	23-24(23.33±1.43)3	22-26(24.29±1.16)7
(Northern Population)	3-6(4.56±0.18)54	4-7(5.01±0.13)94	3-7(5.22±0.23)54	3-7(5.17±0.20)94	19-27(24.17±0.41)54	19-28(24.68±0.29)94
(Osa Population)	3-5(4.00±2.48)3	4-6(4.75±1.52)4	4-5(4.67±1.43)3	5-7(6.00±1.30)4	25(25.00±0)3	25-27(26.25±1.52)4
Central Panamá	5-7(5.75±1.52)4	3-7(5.40±0.55)15	4-5(4.75±0.80)4	5-7(5.47±0.35)15	22-25(23.75±2.00)4	22-25(24.33±0.50)15
Colombia	4-7(5.11±0.32)27	4-7(5.47±0.32)30	3-7(4.70±0.42)27	4-7(5.30±0.28)30	22-26(24.04±0.46)26	22-27(24.87±0.42)30
Ecuador	4.5(4.60±0.68)5	5-6(5.25±0.80)4	5(5.00±0)5	6-7(6.50±0.92)4	24-27(25.60±1.41)5	24-26(25.50±1.59)4
(Southern Population)	4-7(5.11±0.28)36	3-7(5.43±0.25)49	3-7(4.75±0.32)36	4-7(5.45±0.22)49	22-27(24.23±0.43)35	22-27(24.76±0.31)49
Totals	3-7(4.75±0.16)93	3-7(5.14±0.12)147	3-7(5.02±0.18)93	3-7(5.29±0.18)147	19-27(24.22±0.29)92	19-28(24.75±0.22)147

Table 4. Variation in prefoveals, subfoveals, and postcanthals in Bothrops nasuta (explanations as for Table 2).

	Prefoveals		Subfoveals		Postcanthals	
	Males	Females	Males	Females	Males	Females
Mexico	-	3-6(5.00±2.25)2	-	2-3(2.75±0.80)2	-	1(1.00±0)2
Guatemala	3-4(3.14±0.21)7	4-8(5.73±0.46)11	1-3(2.00±0.23)7	2-4(2.36±0.26)11	1(1.00±0)7	1-2(1.18±0.26)11
Honduras	3-8(4.80±2.39)3	4-9(6.00±0.50)13	2-3(2.40±0.68)3	2-5(2.62±0.29)13	1(1.00±0)3	1-2(1.08±0.55)13
Nicaragua	4-8(6.17±1.40)3	5-11(8.13±1.92)4	1-2(1.67±0.54)3	2-7(3.38±1.48)4	1-2(1.17±0.43)3	1-2(1.38±0.43)4
Costa Rica	2-9(4.62±0.35)37	3-12(6.11±0.28)57	1-4(2.09±0.14)37	1-5(2.42±0.14)57	1-2(1.14±0.08)37	1-2(1.61±0.09)57
Western Panama	5-7(6.17±0.79)3	4-10(6.64±1.00)7	2-3(2.33±0.54)3	2-4(2.29±0.35)7	1(1.00±0)3	1-2(1.79±0.25)7
(Northern Population)	2-9(4.61±0.30)53	3-12(6.15±0.22)94	1-4(2.09±0.11)53	1-7(2.48±0.11)94	1-2(1.10±0.06)53	1-2(1.47±0.07)94
(Osa Population)	3-8(4.67±0.96)3	3-7(5.00±1.09)4	1-3(2.00±0.66)3	2-3(2.13±0.37)4	1(1.00±0)3	1-2(1.25±0.39)4
Central Panama	5-8(6.13±1.13)4	3-11(6.23±0.78)15	1-3(2.13±0.54)4	1-3(1.97±0.11)15	1-2(1.50±0.45)4	1-2(1.43±0.19)15
Colombia	3-9(4.96±0.42)27	3-11(6.27±0.45)30	1-3(2.09±0.13)27	1-5(2.38±0.17)30	1-2(1.07±0.07)27	1-2(1.30±0.12)30
Ecuador	3-5(3.90±0.53)5	5-8(6.50±0.89)4	1-3(2.00±0.48)5	1-3(1.88±0.54)4	1-2(1.20±0.37)5	1-2(1.25±0.16)4
(Southern Population)	3-9(4.94±0.36)36	3-11(6.28±0.36)49	1-3(2.08±0.12)36	1-5(2.21±0.14)49	1-2(1.14±0.08)36	1-2(1.34±0.10)49
Totals	2-9(4.74±0.22)92	3-12(6.16±0.19)147	1-4(2.08±0.08)92	1-7(2.38±0.09)147	1-2(1.11±0.05)92	1-2(1.42±0.06)147

Table 5. Variation in supralabials, infralabials, and oculabials in Bothrops nasuta (explanations as for Table 2).

	Supralabials		Infralabials		Oculabials	
	Males	Females	Males	Females	Males	Females
Mexico	-	10-11(10.25±0.80)2	-	12-13(12.25±0.80)2	-	2(2.00±0)2
Guatemala	9-10(9.21±0.25)7	9-10(9.64±0.22)11	10-12(11.21±0.33)7	11-13(11.77±0.28)11	2(2.00±0)7	2(2.00±0)11
Honduras	9-10(9.33±0.54)3	9-11(9.92±0.30)13	10-12(11.00±0.94)3	10-13(11.92±0.28)13	1-2(1.60±0.68)3	1-2(1.92±0.11)13
Nicaragua	9(9.00±0)3	9-10(9.75±0.39)4	11-12(11.50±0.57)3	12-13(12.25±0.39)4	1-2(1.83±0.27)3	2(2.00±0)4
Costa Rica	9-10(9.22±0.10)38	8-11(9.56±0.01)57	10-12(11.04±0.16)38	10-13(11.76±0.12)57	1-3(1.89±0.08)37	2-3(2.04±0.04)57
Western Panama	9-10(9.17±0.43)3	9-10(9.46±0.31)7	10-11(10.33±0.54)3	10-12(10.86±0.50)7	2(2.00±0)3	2(2.00±0)7
(Northern Population)	9-10(9.20±0.08)54	8-11(9.64±0.09)94	10-12(11.05±0.14)54	10-13(11.75±0.10)94	1-3(1.90±0.07)53	1-3(2.02±0.03)94
(Osa Population)	8-10(9.00±0.66)3	9-11(10.00±0.45)4	10-12(10.67±0.86)3	11-13(12.00±0.45)4	2(2.00±0)3	2-3(2.25±0.48)4
Central Panamá	9-10(9.13±0.30)4	8-10(9.57±0.21)15	10-13(11.38±0.89)4	10-12(11.60±0.21)15	1-3(2.00±0.45)4	1-2(1.97±0.07)15
Colombia	8-11(9.15±0.12)27	9-10(9.52±0.13)30	10-12(10.65±0.16)27	10-13(11.73±0.18)30	1-3(1.94±0.13)27	1-4(2.20±0.13)30
Ecuador	9-10(9.10±0.23)5	9-10(9.25±0.39)4	9-11(10.30±0.48)5	11-12(11.63±0.43)4	2(2.00±0)5	2-3(2.38±0.43)4
(Southern Population)	8-11(9.14±0.10)36	8-10(9.51±0.10)49	9-13(10.68±0.17)36	10-13(11.68±0.13)49	1-3(1.96±0.11)36	1-4(2.14±0.09)49
Totals	8-11(9.18±0.06)93	8-11(9.60±0.07)147	9-13(10.89±0.11)93	10-13(11.73±0.08)147	1-3(1.92±0.06)92	1-4(2.06±0.04)147

oculabials are more than two is greater in Colombian and Ecuadorian specimens (21.2%) than in the remainder of the range (4.1%).

Supralabials and Infralabials. - The numbers of supralabials and infralabials average more in females than in males over the entire range (Table 5). All but one specimen (UMMZ 91078) have the first infralabials in contact.

Ventrals. - The number of ventral scales is slightly, but significantly higher in females than in males (Table 2) considering the range as a whole. A relatively high number of ventral scales is present in specimens of *B. nasuta* from western Panamá northward to México (129-145, $\bar{x} = 137.68 \pm 0.42$). A relatively low number exists in specimens from central Panamá southward to Ecuador (123-143, $\bar{x} = 132.15 \pm 2.58$).

Subcaudals. - As is usual in snakes, the subcaudals are more numerous in males than in females (Table 2), correlating with their greater relative tail length (Table 7).

Dorsal Scale Rows. - The dorsal scale rows usually number 25-23-19 (see description). Specimens from the Península de Osa are unusual, however, in possessing atypically high dorsal scale row counts (Table 6). Only one of the seven specimens available from there has the above-mentioned count. Two specimens have 25-25-19 rows, three have 27-25-19 rows, and a sixth has 29-27-19 rows. The latter specimen has the highest neck and midbody counts of any specimen examined.

Canthals. - All of the specimens that possess more than one canthal are from central Panama. Of 19 specimens from this area, 7 have two canthals on at least one side of the head; three specimens have two on both sides of the head.

Postcanthals. - Females show a higher incidence of two postcanthals (instead of one) than do males throughout the range (Table 4), with the exception of the sample from central Panamá. Viewed over the entire range, the differences are significant.

Color and Pattern. - Various aspects of color and pattern in *B. nasuta* vary individually, ontogenetically, sexually, and geographically.

There is considerable intrapopulational variation with some individuals being brightly marked on the head and body, whereas others are almost unicolor (see description).

The only series of specimens from a single locality from which adequate notes on ontogenetic color variation could be taken consists of twenty specimens from the Río Patia in southern Colombia (AMNH 107912-13, 109794-811). The juvenile specimens are noticeably brighter in color and more distinct in pattern than are the adults. In larger specimens the brownish gray ground color is basically the same but the brownish black to black dorsal blotches are faded and the whitish border of these blotches is indistinct. The fading of the pattern begins on the lateral portion of the dorsum and proceeds dorsad. The vertebral pale line is bright in the young and gradually fades in larger specimens, particularly females, until, in some specimens the line disappears altogether. In juveniles the dorsal blotches are discrete and well-defined, except for the first two or three blotches, which are reduced to small spots. As the animals increase in size, the blotches gradually fragment into two portions, which are laterally displaced from the middorsal line. This fragmentation and lateral displacement of the dorsal blotches proceeds from anterior to posterior.

Males generally possess a more contrasting facial and dorsal coloration than do females, although occasional dark male specimens are also seen. Males average more body blotches than do females and the values for the entire sample are significantly different (Table 1).

A living specimen from Ecuador in the senior author's private collection exhibits a peculiar temporary coloration prior to ecdysis. The animal is grayish

Table 6. Variation in dorsal scale rows in Bothrops nasuta (explanations as for Table 2).

	Males	Females
México	-	25(25.00±0)2
	-	23(23.00±0)2
	-	19(19.00±0)2
Guatemala	25(25.00±0)7	25-27(25.19±0.41)11
	23(23.00±0)7	23(23.00±0)11
	19-20(19.15±0.35)7	19(19.00±0)11
Honduras	25(25.00±0)2	25-27(25.36±0.49)12
	23(23.00±0)2	23-25(23.18±0.37)12
	19(19.00±0)2	19(19.00±0)12
Nicaragua	25(25.00±0)3	25(25.00±0)4
	23(23.00±0)3	23(23.00±0)4
	19(19.00±0)3	19(19.00±0)4
Costa Rica	23-27(24.92±0.52)39	23-27(25.08±0.14)57
	21-23(22.81±0.20)39	21-25(22.99±0.11)57
	19-20(19.03±0.32)39	17-21(19.01±0.10)57
Western Panamá	25(25.00±0)3	23-25(24.69±0.86)6
	23(23.00±0)3	23(23.00±0)7
	19(19.00±0)3	19(19.00±0)7
(Northern Population)	23-27(24.93±0.18)54	23-27(25.09±0.12)92
	21-23(22.85±0.14)54	21-25(23.02±0.08)93
	19-20(19.04±0.05)54	17-21(19.00±0.06)93
(Osa Population)	25-27(25.70±2.87)3	25-29(27.07±2.60)4
	23-25(24.37±2.87)3	25-27(25.53±1.60)4
	19(19.00±0)3	19(19.00±0)4
Central Panamá	23-25(24.53±1.60)4	23-25(24.75±0.39)15
	22-23(22.68±1.43)3	23(23.00±0)15
	19(19.00±0)4	19(19.00±0)15
Colombia	25(25.00±0)27	23-27(25.44±0.36)30
	23(23.00±0)27	23-25(23.22±0.11)30
	19(19.00±0)27	19-21(19.12±0.56)30
Ecuador	23-25(24.63±1.11)5	25-27(25.53±1.59)4
	21-23(22.63±1.11)5	23(23.00±0)4
	19(19.00±0)5	19-20(19.26±0.80)4
(Southern Population)	23-25(24.89±0.02)36	23-27(25.20±0.27)49
	21-23(22.91±0.13)35	23-25(23.13±0.14)49
	19(19.00±0)36	19-21(19.09±0.13)49
Totals	**23-27**(24.94±0.13)93	23-29(25.18±0.13)145
	21-25(22.92±0.12)92	21-27(23.12±0.10)146
	19-20(19.02±0.13)93	17-21(19.03±0.06)146

brown dorsally and powder gray ventrally. During the premolt period the ventrals and the first dorsal scale row and the ventral half of the second row turn a bright silver, contrasting markedly with the color of the remainder of the dorsum (Fig. 3).

Size and Proportions. - The average dimensions in head length, head width, head height, total length, and body length are greater in females than in males (Table 7; Fig. 4). Males possess a greater average relative tail length (Table 7), correlated with the higher average number of subcaudals (Table 2). Female specimens appear to be stouter than do males, but this feature is difficult to quantify because of variation caused by preservation.

Sex Ratios. - We sexed 240 specimens of *Bothrops nasuta*. A prevalence of females is present in collections from México southward through central Panamá (64.9% females vs. 35.1% males). The sex ratios in samples from Colombia and Ecuador are more evenly balanced (51.5% females vs. 48.5% males) (Table 1). Considering the number of specimens involved, it seems unlikely that these differences result simply from artifacts of collecting. The reasons for the greater percentage of females in samples from Panamá northward, however, remain obscure.

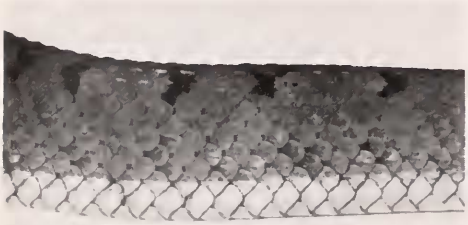

Figure 3. Section of body of a female *Bothrops nasuta* from Ecuador illustrating the marked contrast between the lower ventral color and that of the dorsum that is exhibited prior to ecdysis.

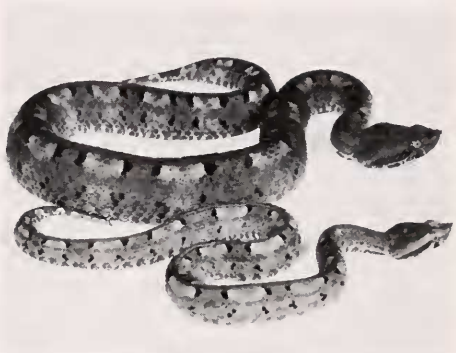

Figure 4. Adult male (lower) and female (upper) *Bothrops nasuta* from northern Honduras illustrating sexual dimorphism in size and the typical color pattern of members of the northern population.

DISCUSSION

On the basis of the foregoing analysis, the following characteristics have been shown to exhibit geographic variation in *Bothrops nasuta*: internasals; nasofrontals; intercanthals; interoculars; oculabials; ventrals; dorsal scale rows; canthals; color and pattern; sex ratios.

These characteristics show differing patterns of variation. The frequency of mutual internasal contact decreases markedly between samples from western and central Panamá. Ventral numbers are highest in the northern section of the range (western Panamá northward) and lowest in the southern section (central Panamá southward). Average numbers of interoculars are not significantly different between the sexes in samples from western Panamá northward, whereas the differenes are significant from that point southward. Central Panamanian specimens are distinctive in having a higher average number of nasofrontals, as well as being the only specimens possessing more than one canthal scale. Panamanian specimens have a higher average number of intercanthals than do specimens from the rest of the range. The preponderance of female specimens from the northern portion of the range south to and including central Panamá is

Table 7. Sexually dimorphic characters of size and proportions in *Bothrops nasuta* (measurements in millimeters - parenthetical numbers indicate range, mean, and sample size).

	Males	Females
Head length	11-24(17.0)93	12-37(22.6)147
Head width	7-15(11.3)93	8-28(14.9)147
Head height	4-10(6.6)93	4.14(8.6)147
Total length	162-463(291.1)88	156-635(349.0)139
Tail length	20-62(36.2)88	16-64(35.7)139
Body length	142-401(254.9)92	140-571(313.4)142
Tail/total length ratio	0.103-0.137(0.124)88	0.092-0.122(0.103)139

in marked contrast to the more even sex ratio in samples from Colombia and Ecuador. Specimens from Colombia and Ecuador have higher average numbers of oculabials than do specimens from the remainder of the range. The Península de Osa specimens are distinctive due to: (1) a higher number of dorsal scale rows on the neck and at midbody; (2) the juvenile tail color persisting into adulthood; (3) the shape and degree of elevation of the internasal scales, and (4) a distinctive dorsal body coloration.

Obviously, the most distinctive specimens are those occurring in the Península de Osa. Due to the small number of specimens available from this area, however, it remains an area in need of critical study. Other, less distinctive geographical groupings may be circumscribed as well. The patterns of variation in the samples of populations of *B. nasuta* outside of the Península de Osa are such that no clear cut distinctions can be drawn (i.e., the patterns of variation are discordant). On the other hand, the pattern of variation in several characters (frequency of mutual internasal contact; number of ventrals; nasofrontals, canthals, and intercanthals; sexual differences in average numbers of interoculars; and sex ratios) is such that a number of changes in those patterns occur in Panamá, with the most obvious changes occuring between western and central Panamá. Specimens from central Panamá, therefore, in general resemble specimens from South America, whereas those from western Panamá resemble specimens to the north (excluding those from the Osa Peninsula).

On the above basis, therefore, we prefer to recognize three distinctive populations of the hognose viper, *Bothrops nasuta*: the northern, Osa, and southern populations. Inasmuch as these populations do not exhibit equivalent levels of divergence, we do not recognize infraspecific taxa. We feel that to do so would tend to obscure the complex relationships we have detailed above. The populations are characterized below.

The Northern Population. - This population extends from southern México southward to the Boca de Almirante area of western Panamá, with the exception of the Península de Osa-Golfito area of southern Costa Rica. This population is characterized by having a greater incidence in the mutual contact of the internasal scales (98.6% of the specimens examined), a higher average number of ventral scales (males, 129-143, $\bar{x}$=136.98; females, 128-145, $\bar{x}$=138.14), a lower average number of nasofrontal scales (males, 22-46, $\bar{x}$=33.77; females, 25-54, $\bar{x}$=35.78), and a lower mean number of oculabials (96.6% of specimens having two or fewer). Typical examples from this population are illustrated in Figure 4.

The Osa Population. - This population is confined to the Península de Osa-Golfito area of southern Costa Rica and possibly adjacent western Panamá. This population is characterized by having a higher mean number of dorsal scale rows at the neck and midbody, the tendency of juvenile tail color to persist into adulthood (especially on the underside of the tail), a lesser degree of eleva-

tion of the anterior portion of the internasal scales, and a tendency for possession of transverse body bands (Fig. 5), as opposed to alternating blotches or spots.

The Southern Population. - This population occurs from Valle de Antón and the Canal Zone in central Panamá southward to Ecuador. This population is characterized by having a relatively low incidence of mutual contact of the internasal scales (52.4% of specimens examined), a lower average number of ventral scales (males, 123-141, $\bar{x}$=130.57; females, 127-143, $\bar{x}$=133.35), a higher average number of nasofrontal scales (males, 25-56, $\bar{x}$=40.14; females, 29-59, $\bar{x}$=42.84), and a higher mean number of oculabials (17.6% of specimens having three or more).

Biogeographic History. - Recently several authors have shown that alternating dry and humid climatic periods and sea level fluctuations occurring during the Pleistocene have had a marked effect on the evolution and distribution of Neotropical vertebrates (van der Hammen, 1961; Haffer, 1969; Vuilleumier, 1971; Duellman, 1979). In addition, several recent taxonomic studies on South American and Central American amphibians and reptiles have shown a close correlation between evolutionary events in the group in question and the paleogeographic events detailed in the above-cited papers (Vanzolini and Williams, 70; Duellmn, 1972; Heyer, 1973; Duellmn and Crump, 1974; Wilson and Mena 1980).

Figure 5. Adult female *Bothrops nasuta* (USCCRE 6391) from Rincón de Osa, Puntarenas Province, Costa Rica, illustrating the dorsal pattern of transverse bands.

Although the evolutionary relationships of the *Bothrops lansbergi* group, to which *B. nasuta* belongs, are imperfectly known, Burger (1971) expressed the opinion that the members of the *lansbergi* group, as well as those of the *godmani* and *nummifera* groups constitute a distinct genus, *Porthidium*. He stated that

"the *lansbergi* and *nummifera* groups diverged independently from the *godmani* group." In addition, he opined that "*Porthidium nasutum*, which is similar to *P. godmani* in some respects and specialized in others, is close to the ancestry of the *lansbergi* group." For these reasons we assume, for the present, that the point of origin of the species *B. nasuta* lies somewhere in Nuclear Central America and, most likely, southern México.

On the basis of information in the above-cited papers, we postulate the following sequence of events to account for the evolutionary history of *Bothrops nasuta*:

1. Movement of the *B. nasuta* stock from the north (probably southern México) into Central America during the upper Pliocene along the eastern humid corridor.
2. Movement of the stock of the Osa population into southern Pacific Costa Rica through low plateaus and/or narrow river canyons in the uplifting Talamanca range during the turn of the Pliocene-Pleistocene.
3. Isolation of the Osa population in the Península de Osa by rising sea levels during the interglacial periods of the Pleistocene.

4. Isolation of the northern and southern populations in wet forest refugia in Caribbean Central America and the Pacific side of Colombia, respectively, during a period of dry forest expansion in the Quaternary.

SPECIMENS EXAMINED

Locality data for each specimen examined are listed below. The data are arranged as follows: alphabetically by country, state (department or province), and locality; alphabetically by the first letter in the abbreviations for the museums, and numerically after each museum abbreviation. Specimens lacking precise locality data are listed in the first most restricted political unit possible. Localities enclosed by quotation marks are not mapped.

The localities and specimens are: COLOMBIA: "Boca de la Raspadura," AMNH 18298-300. *Antioquia*: "Medellín," AMNH 35735; Río Arquía, Belen, LACM 45413; Sabanalarga, Cauca Valley, AMNH 35795. *Cauca*: Quebrada Guanguí, 0.5 km above Río Patía, 100-200 m, AMNH 109794-811; Quebrada Guanguí, Río Patía, 100 m, AMNH 107912-13. *Chocó*: "no specific locality," AMNH 8067-68; Andagoya, MCZ 29255, USNM 124259, Andagoya-Condota area, UMNZ 121043-44; between Andagoya and Condota, UMMZ 121058; vic. Playa de Oro, upper Río San Juan, 200 m, AMNH 108460; Quebrada Taparal, 20 km N Palestina, CAS 119919; Río Atrato, S of Quibdó, USNM 140050; Río San Juan, USNM, 72352; Sierra de Baudó, ANSP 25573-78; trail between Quebrada Bochoramá and Río Tadocito, LACM 45416. *Valle*: Buenaventura, at Rockerfeller Lab, 12 m, TU 18712; km 13 from Buenaventura to Río Calima, 45 m, FMNH 165478, 165893; near Buenaventura on land of Cartón de Colón, TU 18711; Río Calima, Quebrada de la Brea, USNM 124260; Río Calima, 7 km from lumber camp, FMNH 165492, 165495, 165566, 165725-26, 165900; Rio Paposo, Virology Field Station, USNM 151711-12.

"COLOMBIA or ECUADOR": USNM 22422.

COSTA RICA: "Hospital San Juan de Dios," KU 34636; "Costa Rica,"UF 20627, 30709, UMMZ 133893, 133911. *Alajuela*: Cantón de San Carlos, Muelle San Carlos, 65 m, USC-CRE 2711; Cariblanco, UCR 1431; Cataratas de San Ramon, Lado San Carlos, USC-CRE 2754; Ciudad Quesada, 656 m, USC-CRE 2693; Ciudad Quesada, San Roque, 580 m, USC-CRE 2695; San Carlos, FMNH 191789, UMMZ 131327-29; Sarapiquí, 100m, UCR 109, 2990, USC-CRE 2691. *Cartago*: Pavones, nr. Turrialba, 819 m, KU 140087, LSUMZ 36898-99, USC-CRE 2710; Turrialba, 624 m, KU 30982-87, 34876, 34879-80, 35734-35, MCZ 55067-74, UCR 1870; Turrialba, IICA, 600-624 m, AMNH 69722, FMNH 179083, KU 25689, 34635, 34637-38, MCZ 56116, USC-CRE 646; Turrialba, 3 km from IICA on road to Pavones, 630 m, USC-CRE 190. *Guanacaste*: El Silencio de Tilarán, 825-850 m, USC-CRE 6217; 5 km ENE Tilarán, 600 m, KU 36693; Tilaran, 560-562 m, KU 35737-38, USC-CRE 2694, 2712, 7131, 7163. *Heredia*: "no specific locality," UF 30492, 30495, 30498, 31795-96; La Selva, central trail, 60 m, USC-CRE 8291. *Limon*: La Lola, 39 m, KU 34005, UMMZ 117736-37, USC-CRE 127 (2 spec.), 128 (3 spec.), 140 (2 spec.), 162, 203, 207, 655 (2 spec.); Limón, MCZ 19744; Los Diamantes, UMMZ 117738; nr. Penshurst, HSH/RSS 600; Penshurst, UCR 2721-22, 2738-39, 2940-41; Puerto Viejo, UCR 162; 4 km E Puerto Viejo, UCR 308; Suretka, nr. Mt. Mirador, KU 35736; Sipurio, Talamanca, AMNH 17332; Zent, MCZ 11457-58. *Puntarenas*: "no specific locality." UMMZ 83185; Golfito, 5 m, USC-CRE 836; 6.7 km E Golfito, LSUMZ 11652; Rincón de Osa, LACM 114153-54; vicinity of Rincon de Osa, 20-40 m, USC-CRE 6391; Rincon de Osa, Camino del Pacifico, UCR 3310, 3359. *San José*: Puriscal, UCR 110.

ECUADOR: *Esmeraldas*: Playa de Oro, Santiago River, USNM 20625-28; Quinindé, USNM 165317; Río Capapas, MCZ 11169. *Pichincha*: 18 km W Santo Domingo de los Colorados on Chono road, USNM 165320; 5 km W Santo Domingos de los Colorados, USNM 165321; 12 km NW Santo Domingo de los Colorados on Quinindé Road, USNM 165319. USNM 165319.

GUATEMALA: *Alta Verapaz*: Finca Chamá, UMMZ 91077-78. *El Petén*: 12 km NW Chinajá, 130 m, KU 55705; Piedras Negras, USNM 110415; Sayaxché, UCM 22367; Sojío (=Toocog), AMNH 69966-67, 69987; Tikal, 283 m, MCZ 55436-37, UF 13866, 13868-69, UMMZ 117944; 4.8 km S Tikal, KU 157665; 13.5 mi S Tikal, KU 157664; Valontun, 4 km SE Tikal, AMNH 100410. *Izabal*: 12.8 km SE Cayo Piedra, 153 m, ANSP 22149.

HONDURAS: *Atlántida:* Dakota, East Line, MCZ 20247; Jilamo, MCZ 34385; Lancetilla, AMNH 46958-60, MCZ 38781; Sonora Farm, Taujica District, MCZ 20493; Tela, AMNH 46961; Tela, Juliana Farm, MCZ 22023. *Cortés:* La Cumbre, nr. San Pedro Sula, MCZ 32028; San Pedro Sula, MCZ 33332-33. *Snata Barbara:* Santa Barbara, MCZ 27566; Trinidad, MCZ 27565. *Yoro:* Progreso, MCZ 22024, 26872-UMMZ 62522.

MÉXICO: *Chiapas:* Lake Miramar, USNM 136966-67. "Veracruz," ANSP 4873.

NICARAGUA: "vicinity of Poderoso," AMNH 12706. *Matagalpa:* "no specific locality," UMMZ 57654; Hacienda La Cumplida,

900m, UMMZ 117735; 19 km N Matagalpa, UMMZ 116523. *Río San Juan*: Los Sabalos, San Juan River, AMNH 28355. *Zelaya*: Eden Mine, AMNH 7411; Río Huahuashán, Papel Camp, AMNH 70247.

PANAMÁ: "Panama City," MCZ 37115-16. *Bocas del Toro*: Almirante, FMNH 83466, 153847, KU 80247, 112597; 11 km NW Almirante, FMNH 153849, 153851-52, 153999; 12 km NW Almirante, UU 5564. *Canal Zone*: Chico Limpio Divide, 470 m, MCZ 42767; Madden Dam, ANSP 23889; nr. Miramar River, 183 m, MCZ 42768; Pequeni-Esperanza Ridge, 214-610 m, MCZ 42772-81. *Coclé*: El Valle de Antón, 550 m, KU 112596; El Valle de Antón, Finca Acre, FMNH 68054-56. *Panamá*: nr. Boquerón, Candelaria, and Peluca Station, AMNH 68850.

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BELIZE: Xuanantunich (Neill, 1965).

COLOMBIA: *Antioquia*: Segovia (Nicéforo María, 1942); "Urrao" (Nicéforo María, 1938, 1942); Zea District (Posada-Arango, 1889). *Caldas*: "Pueblo Rico" (Nicéforo María, 1938, 1942). *Chocó*: Cabeceras (Rendahl and Vestergren, 1941); Quibdó (Nicéforo María, 1942.

GUATEMALA: *Alta Verapaz*: Panzos (Bocourt, 1868).

MEXICO: *Chiapas*: Rancho Alejandría, Municipio de Juárez (Alvarez del Toro, 1973).

NICARAGUA: "Hacienda de Jericho [=Jerico], 991 m" (Gunther, 1895; Boulenger 1896); "Chontales" (Günther, 1895; Boulenger, 1896). *Río San Juan*: Greytown (Amaral, 1929a).

PANAMÁ: *Canal Zone*: "Cerro Bruja" (Amaral, 1929a; Schmidt, 1933; Dunn and Bailey, 1939).

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